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# The Role of Behavioral Responses to Predators in Modifying Urchins' *(Strongylocentrotus droebachiensis)* Destructive Grazing and Seasonal Foraging Patterns

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## Abstract

We documented spatial and temporal patterns of urchins (*Strongylocentrotus droebachiensis*) and periwinkles (*Littorina littorea*) in three habitats: a persistent *Laminaria longicruris* and *L. digitata* bed; an urchin dominated barrens, and the edge of the kelp bed that formed a boundary between the two. Urchins were rare in the kelp and, when present, always large and well hidden, a pattern we interpret as a response to crab and lobster predation. Urchins were abundant in the barrens, and, in the summer when predaceous fish were active during the day, foraged only at night. We observed the formation of a dense urchin feeding front along the kelp bed edge, and these urchins remained exposed and feeding even during the summer. Laboratory experiments demonstrated that aggregations are an effective defense against some predators, and that the presence of crabs increases the tendency of large urchins to aggregate. We hypothesize that healthy *Laminaria* spp. beds persist because kelp bed associated predators keep urchins at low densities and in hiding. A reduction in predation pressure permits urchin densities to increase to the point where they form aggregations, which provide better defense than hiding. These aggregations then graze destructively on *Laminaria* spp., forming barrens. These barrens seem to be a new, stable configuration of the system.

## Introduction

Large scale disappearance of algal beds from coastal Nova Scotia, Canada and their replacement by urchin-dominated barren grounds has received considerable attention in the last 10 yr. Recent evidence (Mann, 1977; Wharton, 1980) suggests that this pattern of kelp bed destruction by the urchin *Strongylocentrotus droebachiensis* may have occurred along the entire 600 to 700 km Atlantic coast of Nova Scotia. It is of crucial importance for the management of valuable coastal resources, and of interest for our understanding of the dynamic behavior of large scale ecosystems, to determine whether these events represent a catastrophic change of state or are part of a long-term cycle. Earlier studies (Mann and Breen, 1972; Breen and Mann, 1976a, b; Lang and Mann, 1976; Evans and Mann, 1977; Hirtle and Mann, 1978) documented the role of urchins in destroying algal beds and maintaining barrens, and have suggested that the lobster *Homarus americanus* is a keystone predator in this system.

We think that a resolution of questions about the stability of alternate states of this, or indeed of any, ecological system requires an understanding both of the mechanisms that maintain a system in any particular configuration, or domain of attraction (Holling, 1973), and of those that precipitate changes of state. Knowledge of spatial and temporal patterns of abundance and distribution of key species, and the interactions that structure and set limits on these, are important components of this understanding.

We have therefore studied an area at Boutilier's Point in St. Margaret's Bay, Nova Scotia that contains, in a relatively small area, a persistent *Laminaria* spp. bed, urchin-dominated barrens, and a zone in between where urchins actively browse on algae. In one sense, this is a model for the larger system with its extensive barrens along the outer coast of Nova Scotia and its productive kelp beds at the southern end of the province (Wharton, 1980). In another sense it is atypical, since the kelp bed at Boutilier's Point has somehow survived for 10 yr after all other kelp in the neighborhood was destroyed by urchins.

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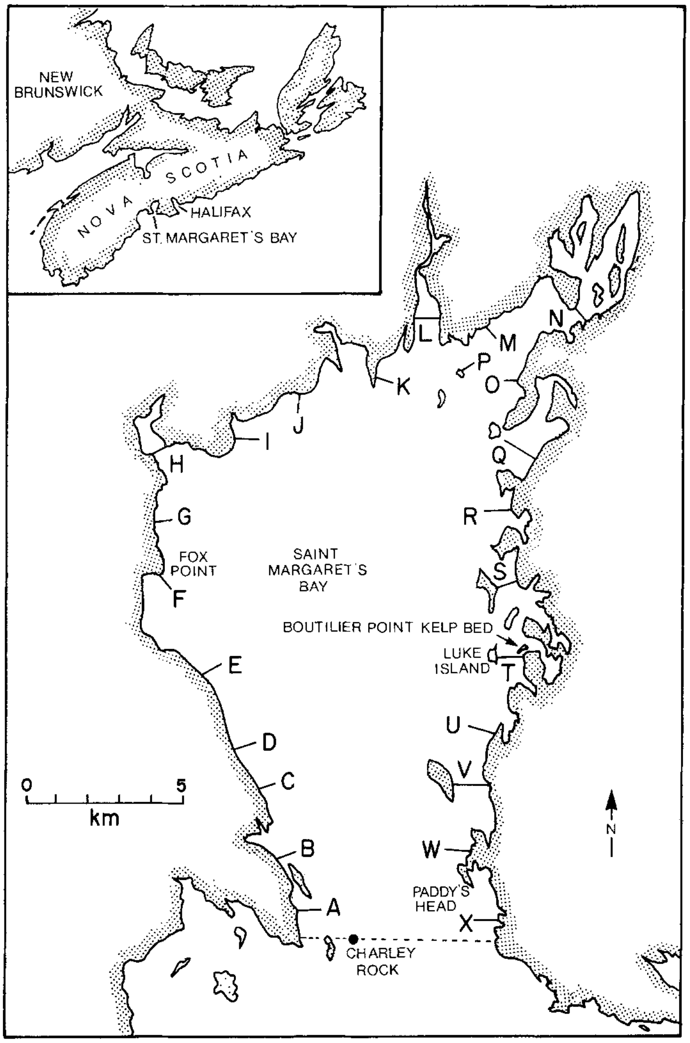

**Fig. 1.** Sketch map showing position of kelp bed at Boutilier's Point, Nova Scotia, Canada. Lettered transects are those used in Mann (1972) to describe the kelp beds before extensive destruction by sea urchins

## Site and Methods

### The Study Area

The study area was a *Laminaria* spp. bed and adjacent barren areas in the shallow subtidal of St. Margaret's Bay, Nova Scotia, Canada. Like other kelp beds previously described from this area (Mann, 1977), the *Laminaria* spp. form a canopy 1 to 2 m above the bottom overlying a variety of other algae. Fig. 1 shows the locations of the study area at Boutilier's Point, and the extent of the bed in 1978.

The substrate in the shallow portion of the bed (1 to 7 m deep) is a combination of large granite boulders mixed with various sized cobbles. In the deeper part of the bed the plants are attached to rock outcrops or small cobbles separated by patches of mud and silt. The bed is well protected from wave surge; the configuration of the bay and several islands immediately to the west protect it from most directions.

To the south the bed is replaced by "barrens", i.e., boulders and cobbles covered by encrusting coralline algae, occasional clumps of mussels *Modiolus modiolus,* and abundant sea urchins *Strongylocentrotus droebachiensis.* In 1968 this entire area was covered by a *Laminaria* spp. -dominated kelp bed (Mann, 1972) but subsequently dense aggregations of sea urchins destroyed the beds, as described in Breen and Mann (1976a). For some reason not fully understood, the kelp bed in the study area has persisted as a remnant of a once much larger bed.

For purpose of sampling and description, we recognize 3 major habitats: the kelp bed, the urchin dominated barrens and a 2 m-wide edge zone, where the other 2 habitats intersect.

### Field Sampling

On each sample date in each habitat, we collected urchins and periwinkles from 10 quadrats of 0.25 $m^2$ placed haphazardly several meters apart. A quadrat frame was dropped from midwater as a diver swam above the sampling area. Quadrats within the kelp bed were at least 10 m from the edge of the bed. All urchins and periwinkles in plain view and not sheltered on more than one side were considered exposed and placed in a separate plastic bag. We then made an exhaustive search of the quadrat for urchins and periwinkles sheltered in cracks in the rocks, under rocks, and under and among algae. We measured urchin diameter and periwinkle length in the laboratory, and weighed all individuals (blotted wet weight). Based on field observations of predator behavior, this procedure provided density and size estimates of herbivores exposed to visual predators such as crabs, lobsters, and fish, and those sheltered from such predators.

We censused starfish within 1 m of either side of a 100 m transect line through the barrens, and recorded the species, length of longest arm, and food items held against the mouth. We noted the relative abundance of crabs and fish on each survey, and, in the spring of 1980, estimated their density in the barrens and along the edge on a series of weekly surveys.

### Laboratory Experiments

All urchins used in the laboratory experiments came from the Boutilier's Point study area, and we performed experiments in 0.6 x 1.0 m tanks supplied with running sea water. These were designed to test the aggregating response of large ($>$ 20 mm) and small ($<$ 20 mm) urchins both to other urchins, and to a predator, the crab *Cancer irroratus.* Any group of 2 or more urchins in physical contact was considered an aggregation. Large and small urchins were introduced into a tank in the desired proportions, and allowed

30 min to become accustomed to the tank. The position of each urchin and the size and location of all aggregations were then recorded every 10 min for 2 h. The number of small and large urchins in aggregations or as single individuals were then summed separately over all twelve observation periods, and a G test (Sokal and Rohlf, 1969) performed on the resulting contingency tables of summed counts. We performed experiments twice and lumped the sums from both replicates into one contingency table.

We also placed individual crabs (*Cancer irroratus*) in tanks with aggregated, hidden, and exposed urchins, and counted the number of crab attacks on each category in a 100-min period. We considered any attempt by a crab to grasp or break open an urchin an attack. This experiment was replicated 4 times.

These experiments were performed in November and December, when water temperature averaged 2° to 3 °C.

## Results

### Kelp Bed

We found urchins in the kelp bed in January 1977, but never after that. Miller and Mann (1973) stated that in St. Margaret's Bay in 1968, just before the onset of widespread kelp bed destruction by urchins, their average density was 36.8 $m^{-2}$. A reexamination of the data (W. G. Wharton, unpublished data) showed that the dense kelp beds contained less than 10 $m^{-2}$, and the partially grazed areas were characterized by much higher densities. Wharton (1980) has also found that an extensive healthy kelp community in Yarmouth County, Nova Scotia contains very few urchins, and that destructive grazing is preceded by a sharp rise in population density. The Boutilier's Point kelp bed, with its extremely low urchin densities, thus seems typical of persistent, *Laminaria* spp.-dominated kelp beds.

Periwinkles (*Littorina littorea*) are present in densities ranging from 21 to 133 $m^{-2}$. More are hidden than exposed, both at night and during the day. We found urchins in the bed hidden only in deep crevices in the rocks, but never found periwinkles so hidden. They were always in folds of *Laminaria longicruris* blades and in understorey algae.

### Barrens

The barrens at Boutilier's Point had relatively high densities (20 to 70 $m^{-2}$) (Fig. 2) of small to medium sized urchins (15 to 30 mm diam.) (Fig. 3). They were randomly distributed and never formed large aggregations. *Littorina littorea* was present at relatively constant densities of about 20 $m^{-2}$ and most of the population was exposed at all times. The population consisted of a uniform size class of 20 to 30 mm length.

### Edge zone

The edge zone is a strip between the kelp and the barrens, about 2 m wide, which forms a distinct habitat. It contains urchins, kelp, and predators, such as crabs and fish, which inhabit the kelp bed and forage there and along the edge. Urchin densities fluctuated over time from scattered individuals (5 $m^{-2}$) to dense aggregations (100 $m^{-2}$) of large individuals (Figs. 4 and 5). As in the barrens, exposed urchins are usually larger than

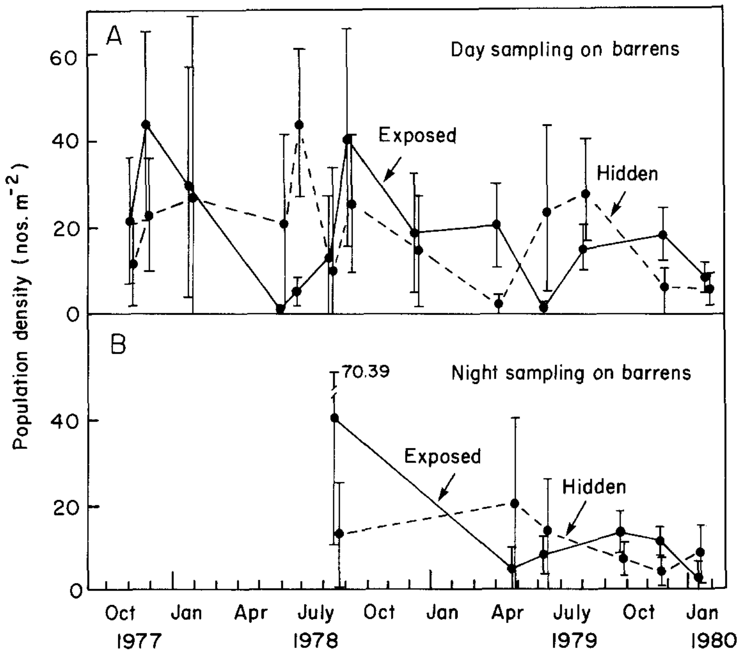

**Fig. 2.** *Strongylocentrotus droebachiensis*. Mean population density of sea urchins on urchin-dominated barren grounds at Boutilier's Point, Nova Scotia, 1977-1980. Each point represents the mean of 10 quadrats of 0.25 $m^2$. The vertical bars give 95% confidence limits on the mean. Exposed and hidden urchins plotted separately. A: day samples; B: night samples

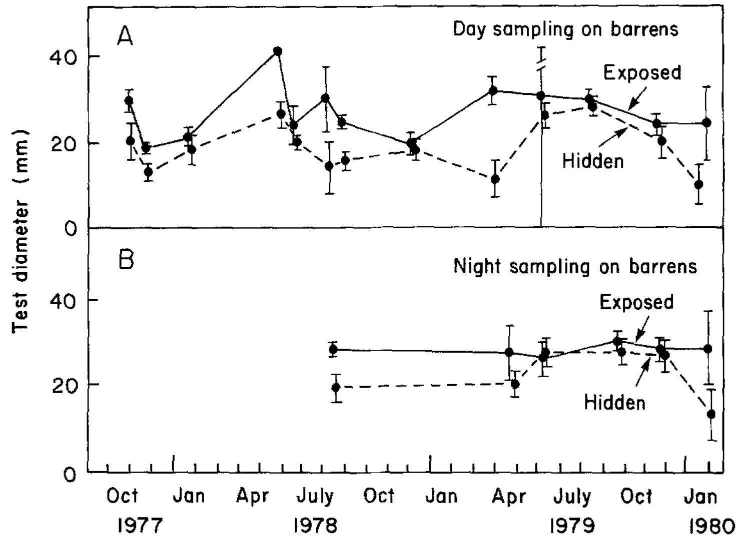

**Fig. 3.** *Strongylocentrotus droebachiensis.* Mean test diameter (mm) of samples of sea urchins taken from urchin-dominated barren grounds at Boutilier's Point, Nova Scotia, 1977-1980. Each point represents the mean of 10 samples of 0.25 $m^2$ and vertical lines represent 95% confidence limits. Exposed and hidden urchins plotted separately. A: day samples; B: night samples

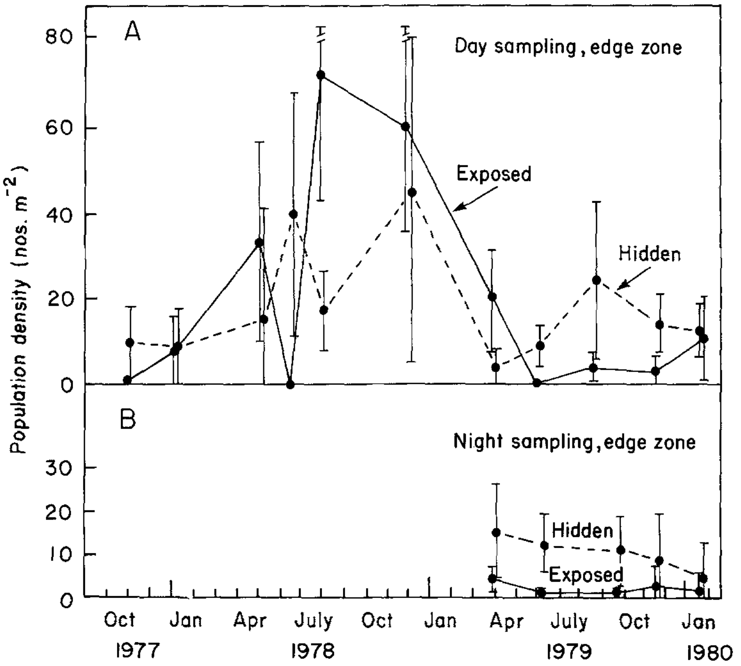

**Fig. 4.** *Strongylocentrotus droebachiensis.* Mean population density of urchins in the edge zone. All other information as in Fig. 2. A: day samples; B: night samples

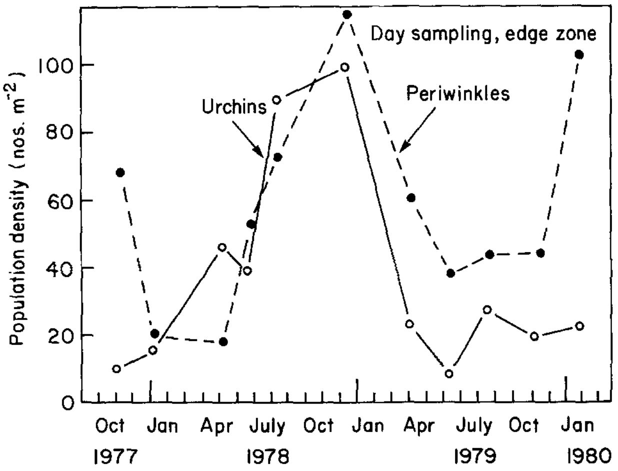

Fig. 5. Mean population density of urchins *Strongylocentrotus droebachiensis* and periwinkles *Littorina littorea* in the edge zone, Oct. 1977 to Jan. 1980

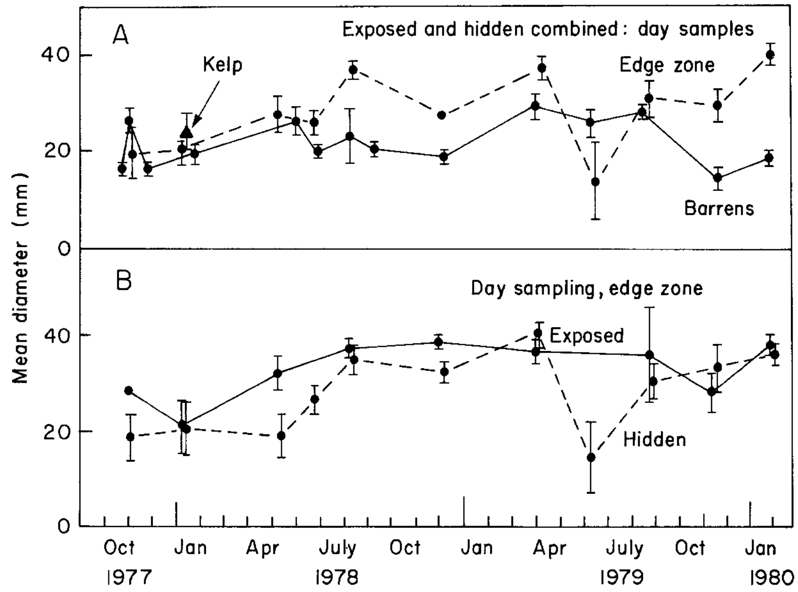

**Fig. 6.** (A) *Strongylocentrotus droebachiensis*. Comparison of mean test diameter (mm) of urchins in the edge zone with those in the barrens sampled by day. Note also an entry for the one occasion urchins were found in kelp. (B) Mean test diameter (mm) of exposed urchins compared with hidden urchins in day samples in the edge zone

those in hiding (Fig. 6), though this pattern changes during the formation of dense aggregations (see below). During the 3 yr of our study, the edge was sharp and well defined, even during periods of urchin aggregation and destructive grazing.

Periwinkle densities along the edge also fluctuate widely (Fig. 5), and more than half the population is exposed at any one time. As in the other habitats, only relatively large periwinkles of 20 to 30 mm length were present.

The population density of both sea urchins and periwinkles increased by a factor of 5 to 10 in the edge zone between January 1978 and January 1979 (Fig. 5). This period was characterized by dense urchin feeding aggregations whose destructive grazing moved the edge several meters into the bed. Urchin and periwinkle densities then declined precipitously over the next 6 months. Accompanying this peak of density were marked changes in the size distribution of the urchins, though not of the periwinkles. Prior to June 1978 the urchins at the edge were only slightly larger than those on the barrens, but from June 1978 to April 1979, during the period of peak abundance, the average size of urchins at the edge was about 50% greater than on the barrens (Fig. 6A). A comparison of exposed and hidden urchins at the edge (Fig. 6B) shows that prior to the increase in population density, hidden urchins were small, but during the period of high density there was very little difference in size between exposed and hidden urchins. The 2 to 3 month period over which this size increase of hidden urchins occurred was too short for it to be accounted for by growth of resident urchins. Therefore during this period there must have been an immigration of larger urchins and the smaller urchins must have left the edge zone.

### Seasonal Variability

*Barrens.* Fig. 2A shows daytime densities of exposed and hidden urchins on the barrens, and Fig. 7A shows the proportion exposed. The proportion exposed during the day is consistently higher during the winter, and there is a period each summer when virtually all urchins are in hiding. Figs. 2B and 7A show that the nighttime foraging pattern is the reverse of the daytime pattern, i.e., urchins tend to forage more at night during the summer.

Hidden urchins were always smaller than those exposed (Fig. 3). A one tailed sign test on the mean sizes of exposed and hidden urchins shows that this tendency for hidden urchins to be smaller is significant at the 0.001 level for day samples and the 0.1 level for night samples.

*Edge.* Figs. 4 and 7B show that urchins along the edge of the bed, as do those on the barrens, exhibit a pattern of daytime hiding during the summer, although nocturnal foraging occurred only during the summer of 1978 and not in 1979 or 1980. During the summer of 1978, urchins along the edge remained hidden during the day for only 1 to 2 months, while all other instances of summer hiding, both on the barrens and along the edge, lasted 3 to 4 months. This shortened period of daytime hiding along the edge coincided with the formation of a dense feeding aggregation of urchins in this zone. Other workers (e.g., Breen and Mann, 1976a) have recorded dense populations of urchins ("fronts") which remained exposed at all times and ate their way steadily into the edge of a kelp bed.

Exposed urchins along the edge were larger than hidden ones (Fig. 6) (P = 0.1, one tailed sign test).

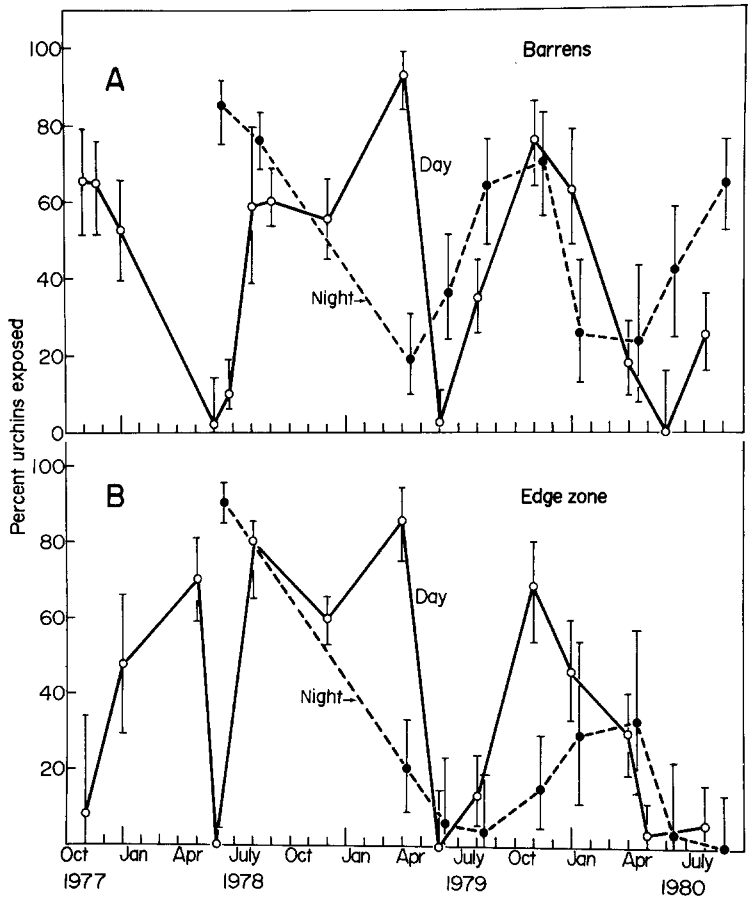

**Fig. 7.** *Strongylocentrotus droebachiensis*. Proportion of urchins exposed in day and night quadrat samples. A: barrens samples; B: edge zone samples

**Table 1.** Percentage of prey in starfish diets, of those found feeding

| | | Day | Night |
|---|---|---|---|
| Sea Urchins | *Strongylocentrotus* | 46 | 31 |
| Detritus | | 33 | 54 |
| Gastropods | (various) | 8 | 4 |
| Periwinkles | *Littorina littorea* | 3 | 11 |
| Mussels | *Modiolus modiolus* | 3 | 0 |
| Limpets | *Puncturella noachina* | 2 | 0 |
| Chiton | *Ischnochiton ruber* | 2 | 0 |
| Tube worms | *Spirorbis* sp. | 1 | 0 |
| Bivalve | (unidentified) | 1 | 0 |
| Starfish | (unidentified) | 1 | 0 |
| | | 100% | 100% |
| | | $n = 491$ | $n = 100$ |

When results from all samples at all the sites were combined we found that the probability that the size of hidden urchins was equal to, or larger than, the size of exposed urchins was less than 0.05.

## Urchin Predators

Urchins are preyed on by several species of vertebrate and invertebrate predators, both in the barrens and along the edge of the bed. We found urchins in the guts of several specimens of wolffish (*Anarhichas lupus*) and American plaice (*Hippoglossoides platessoides*). We observed starfish (*Asterias vulgaris*, *A. forbesi*, and *Henrichia sanguinolenta*) and crabs (*Cancer irroratus* and *Carcinides maenas*) feeding on urchins in the barrens and along the edge of the bed. Lobsters (*Homarus americanus*), and cunner (*Tautoglabrus adspersus*) are known to eat urchins (Johanssen, 1925; Breen and Mann, 1976b; Evans and Mann, 1977;), but we did not observe this in the field.

We quantified the role of starfish as predators by identifying the prey of 100 starfish during night dives and almost 500 during day dives. Table 1 shows that

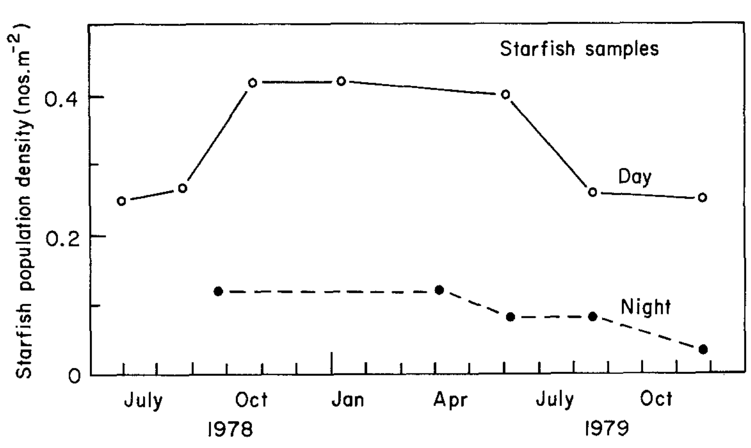

**Fig. 8.** Populations density of all species of starfish exposed in the barrens, day and night samples recorded separately. Samples were taken on a 2 m wide transect, 100 m long

urchins were the most common prey during the day and the second most common at night. Fig. 8 shows that the density of foraging starfish was always much higher during the day, and Table 1 shows that the percent of starfish with detritus in their mouth was significantly higher at night ($P < 0.001$; test for equality of two percentages, Sokal and Rohlf, 1969, p 607). These data suggest that starfish prey is in a more advanced state of digestion at night, and that starfish feed predominantly during the day. This in turn implies that urchins are starfish's major prey.

The seasonal abundance and diurnal activity patterns of predators lead to an important difference in predation pressure between the winter, with its short days and long nights, and the summer, with its long days and short nights. The 3 fish species mentioned above are completely absent from the nearshore in winter, and feed only during the day in summer. We saw wolffish and flatfish resting on the bottom at night and never observed them or the cunner foraging at night. Starfish forage during the day, and display no seasonal patterns of abundance (Fig. 8). Crabs and lobsters forage at night and shelter in the rocks during the day (personal observation), and are more active during the summer when water temperature rises from 0 °C to about 10 °C. Thus, predation pressure on urchins is least intense in the winter, with starfish feeding during the short days, and crabs and lobsters at night. Predation pressure is more intense during the summer, with fish present in addition to the winter predators, and probably most intense during the day in this season, because the shortness of summer nights makes crabs and lobsters relatively less important than the fish.

We tested the hypothesis that the seasonal occurrence of daytime urchin hiding (Fig. 7) is associated with the predation patterns described above by monitoring urchin behavior and the abundance of predators along the southern edge of the bed (180 m long) and in the adjacent barrens weekly from April 16 to June 5, 1980. Fig. 7 shows that, in the spring of 1980, daytime hiding began in April on the barrens and in May along the edge of the bed. Fig. 9 demonstrates that the abundance of wolffish and plaice is correlated to water temperature ($r = 0.92$; product moment coefficient), and that their abundance increases sharply in May, when the proportion of urchins exposed during the day drops to almost zero. We observed no such change in the numbers of starfish, lobsters, or crabs during this period. Fig. 10 shows that the increase in fish abundance is highly correlated with the decrease in number of urchin aggregations and individually exposed urchins along the kelp and bed edge, and also with the increase in amount of broken test fragments found along the edge. The majority of the test remains along the bed edge were small crushed fragments, indicative of feeding by the wolffish, which crushes urchins between its upper and lower palate. Lobsters and crabs, in contrast, leave tests that are more nearly intact. The seasonal change in urchin foraging patterns thus seems to be associated with the appearance of wolffish and plaice in the nearshore in April and May.

## Urchin Aggregating Behavior

Our samples on the barrens and along the edge document that hidden urchins were consistently smaller than exposed urchins. To test the hypothesis that this difference is due to behavior, we placed large (> 20 mm) and small (< 20 mm) urchins in tanks with rocks available for shelter. (Urchin densities in all experiments were well below the density (80 m$^{-2}$) at which urchins in the dense feeding aggregation along the edge changed their behavior and remained exposed during the day.) Table 2 shows that large urchins formed aggregations while small urchins took shelter individually under rocks or in crevices, including the corners of the tank. Even when small urchins were recorded as aggregated, they were part of aggregations dominated by large individuals.

Fig. 10 suggests that the presence of predaceous fish affects urchin behavior. We tested the hypothesis that another abundant predator on urchins, the crab *Cancer irroratus*, influenced urchin aggregating behavior, by introducing individual crabs into the experimental tanks with equal numbers of large and small urchins.

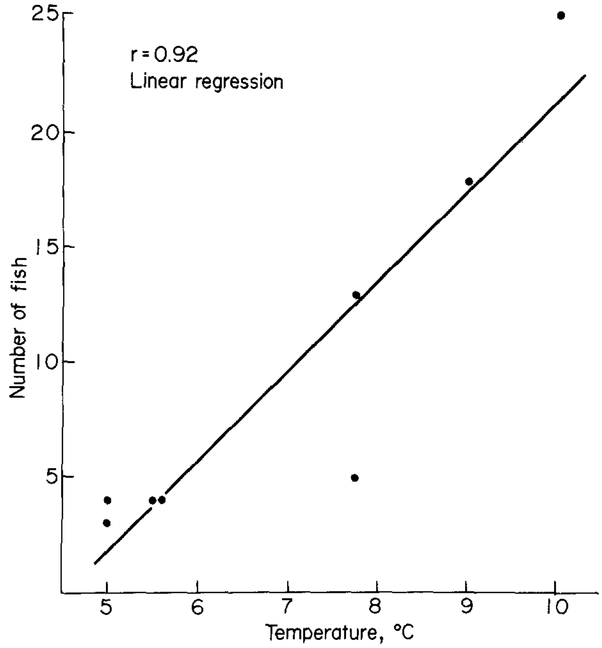

**Fig. 9.** Relationship between water temperature at Boutilier's Pt. and number of wolffish and plaice along the edge of the bed and in the adjacent barrens on weekly surveys from April 16 to June 5, 1980. Each survey included 560 $m^{-2}$

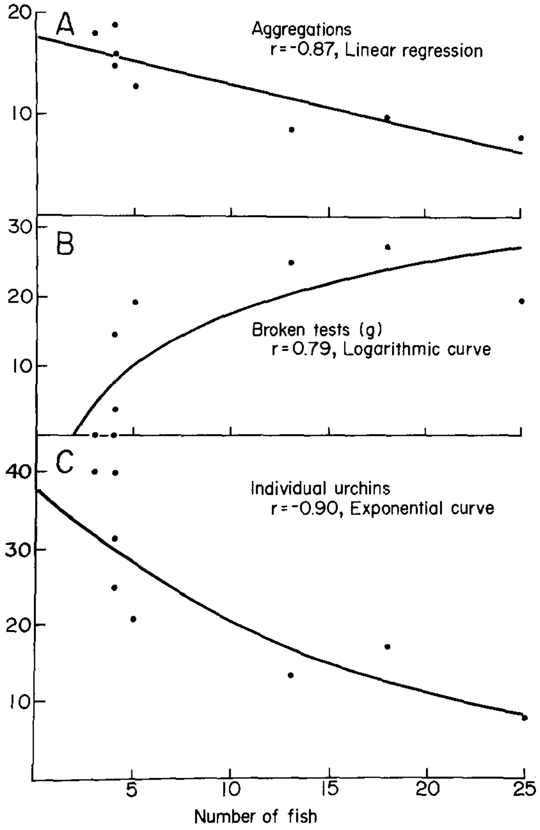

**Fig. 10.** Relationship between number of wolffish and plaice at Boutilier's Pt. (see Fig. 9) and (A) the number of urchin aggregations, (B) the weight in grams of broken test material, and (C) the number of individually exposed urchins along the edge of the kelp bed. Aggregations and exposed urchins were counted in 36 samples of 0.25 $m^{-2}$ each, spaced 5 m apart; broken tests were collected from 5 samples of 0.5 $m^{-2}$ each

**Table 2.** *Strongylocentrotus droebachiensis.* Distributions of large and small urchins in tanks with rocks available for shelter. (Combined totals from 2 experiments)

| | Aggregated | Single |
|---|---|---|
| Large urchins (over 20 mm) | 210 | 86 |
| Small urchins (under 20 mm) | 57* | 188 |
| | P <.0001, G test | |

* 49 of these 57 were aggregated with large urchins

**Table 3.** *Strongylocentrotus droebachiensis.* Response of large and small urchins to the presence of crabs

| | Large urchins | | Small urchins | |
|---|---|---|---|---|
| | Number aggregated | Number exposed singly | Number hidden | Number exposed singly |
| Crabs present | 78 | 2 | 59 | 21 |
| Crabs absent | 20 | 20 | 35 | 5 |

Difference in treatments: large urchins, highly significant P < 0.001, G test. Small urchins, not significant, P = 0.13, G test

Large urchins responded by increasing their tendency to aggregate (Table 3), while small urchins showed no significant difference in behavior.

The fact that large urchins aggregated in response to the presence of crabs suggested this was a defense against crab attack. We tested this hypothesis by placing individual crabs into tanks with large urchins, most of which were aggregated, while the rest were about equally divided between hidden and exposed individuals. Table 4 shows that crabs attacked exposed urchins most frequently, hidden urchins less frequently, and never attacked aggregated urchins. The crabs were unable to get their legs and claws around an urchin in an aggregation. This aggregating defense is probably equally

**Table 4.** *Strongylocentrotus droebachiensis.* Results of attacks by crabs on hidden, exposed, and aggregated urchins in 4 experiments each lasting 100 min

| | Number of attacks by crabs on | | |
|---|---|---|---|
| | Hidden urchins | Exposed urchins | Aggregated urchins |
| Expt. 1 | 2 | 1 | 0 |
| Expt. 2 | 0 | 6 | 0 |
| Expt. 3 | 0 | 3 | 0 |
| Expt. 4 | 4 | 1 | 0 |
| | 6 | 11 | 0 |

**Table 5.** *Strongylocentrotus droebachiensis.* Influence of the presence of small urchins on the tendency of large urchins to aggregate

| Population size structure | Number of large urchins aggregated | Number of large urchins exposed singly |
|---|---|---|
| 17% small urchins | 299 | 32 |
| 50% small urchins | 86 | 57 |

P < 0.0001, G test

effective against predation by small-mouthed fish such as plaice.

The dense feeding aggregation along the edge of the bed was made up almost entirely of large urchins during the peak of density (June 1978 to April 1979). To test the hypothesis that there was a relationship between population size structure and aggregating behavior, we measured the degree of aggregation in experimental populations consisting of either equal proportions of large and small urchins, or 83% large and 17% small urchins. Table 5 shows that a higher proportion of small urchins decreases the tendency of large ones to aggregate.

## Discussion

### Urchin Behavior and Distribution

We found that urchins formed aggregations only along the edge of the kelp bed. Russo (1979) showed for *Strongylocentrotus franciscanus* that, although it formed aggregations in a site having 62% algal cover, it was randomly distributed at a site having only 3.5% algal cover. He showed that the random dispersal was a result of the increased movement in search of food. Mattison *et al.* (1977), working with the same urchin, demonstrated that individuals outside a kelp forest moved greater distances and ate less frequently than those inside it. We also found, as did Garnick (1978), that *S. droenachiensis* forms both feeding and non-feeding aggregations.

Our data indicate, however, that urchins change these generalized distribution patterns seasonally, foraging both night and day on the edge and in the barrens during the winter and only at night on the barrens from approximately May to August. This yearly seasonal change is associated with the onset of fish predation on urchins (See Figs. 7 and 10). Urchins displayed distinct responses to different predators, hiding in the presence of fish and forming aggregations in the presence of crabs (Table 3). Small and large urchins also behaved differentely: small urchins are more likely to hide individually in rocks and less likely to aggregate, both in the presence and absence of predators (Figs. 3 and 6; Tables 2 and 3). This tendency to remain hidden is probably a response to small urchins' susceptibility to a greater range of predators than large urchins, particularly starfish, small-mouthed fish and small crabs. Periwinkles are not subject to the same predation pressures as urchins. The large ones we observed seem to have a refuge in size from all but the larger starfish. Their exposed foraging behavior and abundance in the kelp bed support this view. It is not clear why periwinkles increased in synchrony with urchins along the bed edge (Fig. 5). When urchins feed rapidly, they digest their food very poorly. Perhaps the periwinkles were attracted to this concentration of fragmented, half digested algal material.

Urchins along the kelp bed went through one cycle of dense aggregation and dispersal (Fig. 5). During the period of high density, destructive grazing on *Laminaria* spp. occurred, and the seasonal patterns of distribution described above were modified. Summer daytime hiding lasted only 1 to 2 months (Fig. 7b), probably because the dense aggregation provided a defense against all predators but wolffish. This was also the only instance on which we observed nocturnal foraging along the edge during the summer (Fig. 7b), again because high urchin density provided a defense against kelp bed associated predators that usually keep urchins in hiding (See below).

Urchins' behavioral responses to predators help explain the different distribution patterns we observed in the three habitats. For example, we found urchins in the Boutilier's Point bed on only one occasion, and these were large and well hidden. This, together with Wharton's unpublished data and the historical information from St. Margaret's Bay (See Results, Kelp Bed), suggest that healthy, persistent *Laminaria* spp. beds have very low urchin densities. Since we observed that urchins hide when fish are active in the early summer, we interpret this distribution to be a behavioral response to predation pressure in kelp beds, most probably from crabs, which are abundant in and around kelp beds (Drummond-Davis, 1978) and also possibly from lobsters where they remain abundant (Breen and Mann, 1976b; Mann, 1977). We think it reasonable to suppose that, in the absence of predation pressure, urchins would feed more openly, since *Laminaria* spp. is the preferred food of *Strongylocentrotus droebachiensis* (Vadas, 1968) and since *Laminaria longicruris* we transplanted to the barrens far from the kelp bed in winter (season of low predation) were quickly attacked (within an hour) and fed on openly by urchins.

## Formation of Feeding Fronts

Based on the above data and conclusions, we propose the following scenario for the formation of dense urchin feeding fronts. In a healthy *Laminaria* spp. bed, very low densities of urchins hide in refuges because of predation pressure. Table 4 shows that aggregation is a more effective defense against crab attack than hiding, but aggregation is not a feasible strategy at very low densities, probably because widely separated urchins would be exposed to predation as they sought each other out. It is therefore the combination of very low densities and urchin hiding that constitutes an equilibrium condition with respect to kelp bed predators.

Urchins begin to increase in density (presumably on account of reduced predator pressure, though direct evidence for this is not yet available) and eventually become so abundant that predators find them easily. At high densities, urchins switch strategy, forming exposed aggregations and feeding openly on kelp. Such aggregations are an effective anti-predator strategy, but require high urchin population densities. This scenario requires that there be some critical threshold density, depending on the size of the urchins and the density of their predators, above which urchins will aggregate and begin forming holes in the kelp bed. Our experiments show that the presence of predators (crabs) facilitates the formation of urchin aggregations. Predation thus contributes to kelp bed persistence at low urchin densities but triggers destructive grazing at high urchin densities through a behavioral mechanism.

## Stability and Persistence

The cycle of formation and dispersal of an urchin feeding front at Boutilier's Point is the first documentation of such a cycle in Nova Scotia. We do not know whether the urchins in the front were eaten by predators or simply dispersed quickly into the barrens. The fact that the aggregation disappeared during spring when predators became seasonally abundant in the nearshore zone suggests that intensive predation pressure from fish, particularly the large-mouthed wolffish, might have been responsible for destroying the urchin feeding front. Since this is now one of the few fronts remaining in St. Margaret's Bay, fish from a wide area may have converged on it.

Predators play a much more complex role in the system than previously supposed (Breen and Mann, 1976b; Mann, 1977). Crab and lobster predation in kelp beds keeps urchins at low densities and in hiding. At higher urchin densities the same level of predation contributes to the formation of exposed feeding aggregations as a behavioral response to the predation. Seasonal fish predation, if intense enough, might break up these urchin fronts. If less intense, it temporarily changes urchin foraging behavior in the summer. Depending on urchin density, time of year and type and abundance of predators, predation can thus have a variety of effects, some stabilizing and some destabilizing, because of its influence on both numbers and behavior of urchins. Miller and Mann (1973) showed that even at high urchin densities (36.8 $m^{-2}$) kelp bed production was more than sufficient to feed all the herbivores in the system. This means that healthy kelp beds could support high densities of urchins if they remained hidden but that beyond a threshold density a change in urchin behavior triggered by predators and independent of any further change in urchin density can cause a catastrophic change in system state. In part, this is because urchins in a feeding front may chew through *Laminaria* spp. stipes and destroy plants without having consumed them. This system might thus represent an example of the sort of sudden, qualitative change in system behavior described by Holling (1973) and by catastrophe theory (Jones, 1975; Zeeman, 1976).

This change in system state from *Laminaria* spp. -dominated kelp beds to urchin dominated barrens has been documented in detail for St. Margaret's Bay, Nova Scotia (Breen and Mann, 1976a), and evidence gathered by Wharton (1980) strongly suggests that the same change has recently occurred along much of the 600 to 700 km Atlantic Coast of Nova Scotia. The spatial scale of these events and the relative synchrony of their occurrence argue that this is not an example of the sort of disturbance mediated patch formation that results in a heterogeneous habitat, portions of which are in varying stages of succesion at any one time (Loucks, 1970; Dayton, 1971; Levin and Paine, 1974).

The urchin-predator relationships we have documented do not explain the gradual increase in urchin density in kelp beds prior to destructive grazing (See Results, Kelp Bed). This could be due to a gradual decline in lobster stocks, as proposed by Mann and Breen (1972). The immediate causes of that could be a variety of environmental changes (See Mann, 1977), but the heavy and continuous fishing pressure on stock (the legal size limit is below reproductive size), is most likely a contributing factor.

Mann (1977) questioned whether the change from kelp beds to barrens was irreversible or part of a long-term cycle. Occasional, localized *Laminaria* spp. regeneration occurs in St. Margaret's Bay, adjacent to *Laminaria* spp. that persist in refuges such as the high intertidal or the Boutilier's Point bed (Professor A.R.O. Chapman, personal communication). This regeneration always occurs in summer, when urchins restrict their foraging in reponse to the presence of fish, and the newly settled plants always disappear by fall, when urchins resume daytime foraging. Thus, while urchin's summer behavioral shift in foraging strategy permits some settlement, this does not persist. Chapman (in press) has shown experimentally that urchin densities typical of the barrens (20 to 30 $m^{-2}$) are sufficient to prevent the survival of newly settled *Laminaria* spp. It therefore appears that the urchin-dominated barrens represent a stable state. Some settlement does occur, but, because fish are present only during the late spring and early summer, for this to persist would require a permanent reduction in urchin density.

Such a reduction could occur as a result of an increase in predation pressure on the barrens, but a simple return to the level of predation characteristic of healthy kelp beds will not cause a reversal of the state of the system. Such predation suffices to keep low numbers of large urchins in hiding and to control their density but is not sufficient to reduce populations of small urchins to the point necessary to allow kelp regeneration. Any long term cycle of transitions from kelp bed to barrens and back to kelp bed will therefore involve different mechanisms at each stage of the cycle.

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